Thallus variation in Hormophysa triquetra (C. Ag.) Kuetz. (Fucales, Phaeophyta) in oceanic and estuarine habitats

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Abstract

Hormophysa triquetra (C. Ag.) Kuetz. is one of the few fucoid algae which occur in Australian estuaries. There is a gradient of form variation between oceanic and estuarine environments. The morphological differences result from reduced cell enlargement and cell division in the estuarine compared with oceanic forms. However the pattern of growth and differentiation is the same in all forms so that delimitation of taxonomic sub-groups is not appropriate at this time.

Introduction

Several fucoid algae, including species of *Ascophyllum, Fucus, Hormosira* and *Pelvetia* penetrate into brackish waters, estuaries or salt marshes from rocky ocean shorelines in Europe, North America and New Zealand (Berquist 1959, Chapman 1976, Gibb 1967, South and Hill 1970). In these non-oceanic habitats the algae tend to have narrow fronds, few vesicles, profuse branching, no holdfast and no sexual reproduction. Low salinity has been suggested as the primary cause of these form changes, although Brinkhuis (1976) and Brinkhuis and Jones (1976) show that salt marsh ecads of *Ascophyllum* are the result of tidal emergence combined with high light and high temperatures. In addition, Moss (1971) suggests that the pattern of growth in *Ascophyllum* is irreversibly changed when vegetative regeneration of thalli occurs. In Australia however, the distributions and forms of fucoids in estuaries have not been documented or studied in relation to the environmental factors controlling growth in these habitats.

The wide form variation of *Hormophysa triquetra* (C. Ag.) Kuetzing has resulted in nomenclatural and taxonomic problems, but these have been resolved by Papenfuss (1967) and Womersley (1967). Some of these variations probably are estuarine forms of the species, but this distinction has not been made. Studies by Johnson (1967), Mairh and Krishnamurthy (1970) and Papenfuss (1967) have reported only on the vegetative and reproductive anatomy of the oceanic form of *H. triquetra*. The present study compares the vegetative morphological features of oceanic and estuarine forms of *H. triquetra* in Western Australia.

Material and methods

Material of *Hormophysa triquetra* was collected from the Western Australian coastline and voucher specimens were placed in the Herbarium of the University of Western Australia (UWA). Pieces of thalli from the extremes of the morphological ranges of estuarine (Peel Inlet) and oceanic (Cottesloe reef) environments were fixed in 6% formalin seawater or modified Karpechenko's solution. The tissue pieces were paraffin embedded. Transverse serial sections (4-9 μm) were stained with haematoxylin and mounted in Euparal. The morphologies of apical, mature and vesiculate tissue of oceanic and estuarine forms were compared by measuring tissue and cell (anticlinal and periclinal) dimensions, and by calculating the areas of the vesicular cavities. 160 cells were measured in each of 6 different thalli.

Results

Morphological variation

Although *Hormophysa triquetra* is a perennial species, it is vegetatively dormant and the fronds are denuded in winter. Growth occurs in spring and summer.
Oceanic forms: These forms occur in intertidal pools and in upper sublittoral areas of the limestone reef platforms of the southwestern Australian coast between Shark Bay (24°52′S; 113° 39′E) and Fremantle (32°03′S; 115°45′E). The thallus (Fig. 1A) has triquetrous, twisted fleshy fronds with dentate, winged corners and embedded vesicles. Often, well developed lateral branches are difficult to distinguish from the main axis, resulting in a bushy habit. At north-

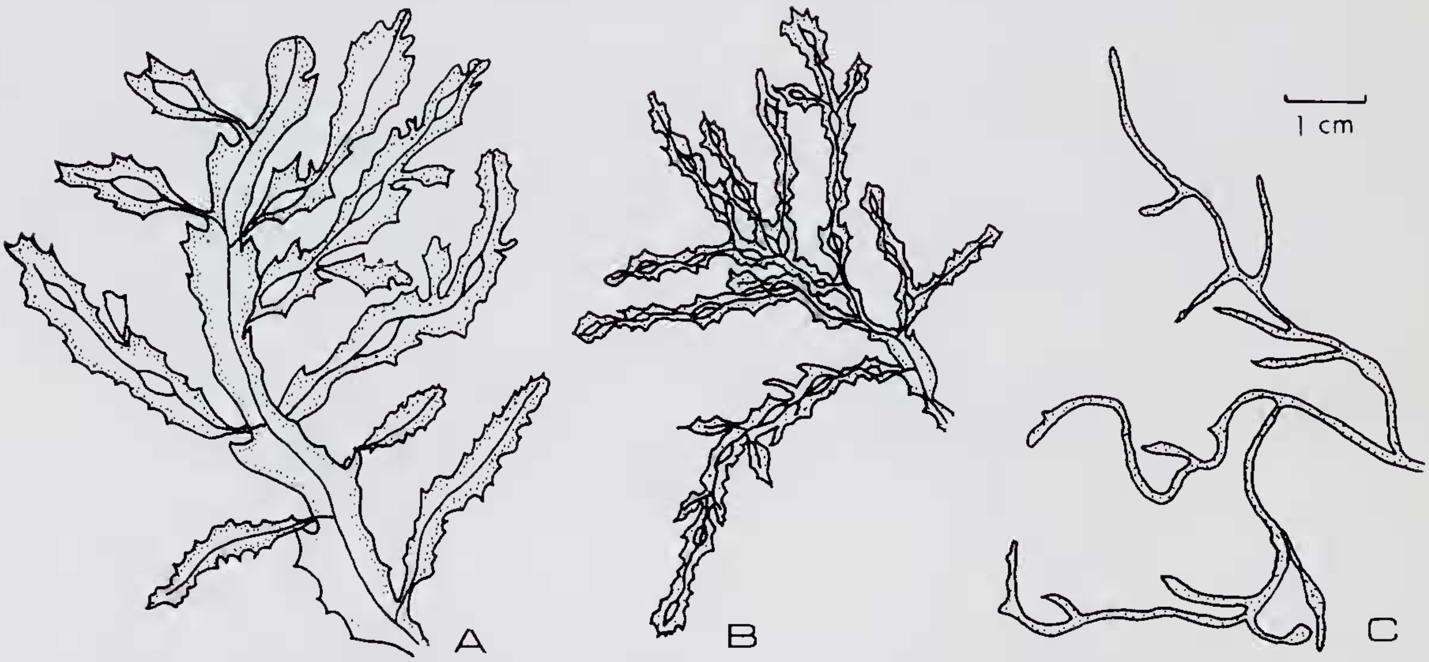

Figure 1.—A.—Portion of southern oceanic form of *Hormophysa triquetra* UWA-A1315. B.—Portion of northern oceanic form. UWA-A32. C.—Portion of estuarine form. UWA-A271.

erly locations, less fleshy specimens have been collected (Fig. 1B). Typical oceanic specimens are UWA-A1302, UWA-A1304, UWA-A1308, UWA-A1313 and UWA-A1315.

Estuarine forms: In the Swan River Estuary (32°03'S; 115°50'E) and Peel Inlet (32°35'S; 115°43'E), the alga grows subtidally to about 1.2 m depth. The thalli are usually attached by a holdfast to limestone rubble or to empty bivalve shells. In the most reduced forms, only portions of the lower thallus anchor the alga in the sandy substrate, or thalli without holdfasts are intertwined with the fronds of another estuarine fucoid, *Caulocystis uvifera*.

The morphology ranges from oceanic forms through reduced wing and narrow frond forms, to reduced spindly almost evesiculate forms. In the latter (Fig. 1C), frond parts near the apex are typically triquetrous, but with a tendency to become rounded lower in the thallus. The spindly forms have intertwining laterals and have a diffuse, entangled form. Typical estuarine specimens are UWA-A271, UWA-A372, UWA-A1037, UWA-A1291, UWA-A1295, UWA-A1298 and UWA-A1299.

Apical morphology

Cell divisions of the meristoderm and cortical layers built out from the faces of the tapered, triangular apical cell results in a triangular apex outline. The structure around the apical cell varies with habitat. Estuarine forms have three simple "horns" of tissue corresponding with the corners of the thallus outline. Thalli from the ocean reefs (Fig. 2A) have elaborate, tapering horns curved over the apical depression. The horns eventually contribute to the dentate wings of the mature thallus margin.

The spiral twisting of the fronds is initiated at the apex (Fig. 2B) because cells are cut off sequentially and slightly obliquely from the apical cell. The spiral branching pattern from the corners of the triquetrous axis results from the successive initiation of lateral initials from the faces of the main apical cell. In oceanic forms (Fig. 2C), a wing of tissue overlies the entire young lateral branch. The basic spiral, monopodial growth pattern is the same in all forms of *Hormophysa triquetra*.

Mature frond and vesicle morphology

In both vesiculate and non-vesiculate areas of the mature fronds the oceanic form has larger cortical cells than the estuarine form (Fig. 3), although the dimensions of the meristoderm cells are similar in both forms. Conceptacular cavities occur in the oceanic form, but none occur in the most reduced of the estuarine forms.

Vesicles occur at irregular intervals along the fronds of both forms, but the estuarine forms have fewer vesicles. Increased cell division in the thallus surface layers ruptures the medulla and part of the inner cortex to form the vesicles cavity (Fig. 2D). The area of the vesicular cavities in the oceanic form ($\bar{x}$ 2.46 mm^2) is twice that of the vesicular cavities in the estuarine form ($\bar{x}$ 1.21 mm^2). The width of the vesicular cortex in the oceanic form ($\bar{x}$ 0.283 mm) is considerably thinner than in non-vesiculate areas of the thallus ($\bar{x}$ 0.388 mm), in contrast to the vesicular cortex of the estuarine form ($\bar{x}$ 0.199 mm) which is thicker than the non-vesicular cortex ($\bar{x}$ 0.153 mm). In both forms the inner cortex is distorted tangentially, and particularly in the oceanic form there is also rupture and loss of inner cortex cells. The

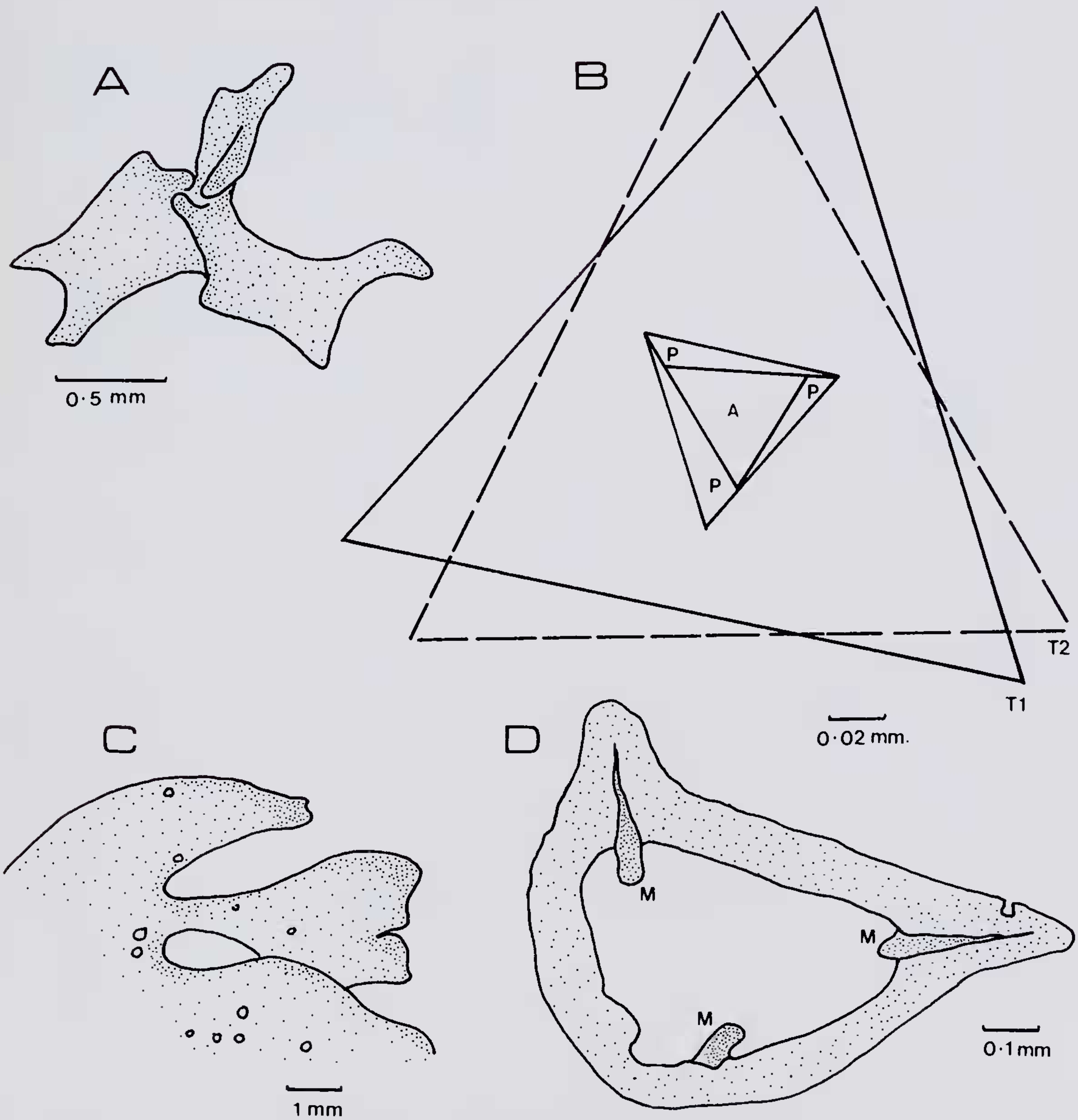

Figure 2.—A.—Top view of oceanic thallus apex of *Hormophysa triquetra* showing twisted horns over apical depression. B.—Diagrammatic outline of spiral apical growth pattern. A, apical cell; P, primary segments of apical cell division; T1 and T2, successive thallus outlines. C.—Oceanic form lateral branch apex with wing of parent thallus. D.—Transverse section of vesicle in estuarine form. M, remnant strands of medulla.

meristoderm and outer cortex cells have the same shape and size in both vesicular and non-vesicular areas since it is cell division in these tissues which forms the vesicles.

Discussion

The form variation of *Hormophysa triquetra* between oceanic and estuarine environments follows the same trend as reported for other fucoid species in similar environments. Perhaps the same environmental factors cause similar types of morphological responses. As with other fucoids, the form variation of *H. triquetra* is a graded response suggesting that the factors controlling differentiation and form are quantitative rather than qualitative.

The morphological differences in *Ascophyllum* are attributed by Moss (1971) to fewer meristoderm cell divisions in reduced forms. In *Hormophysa triquetra* estuarine form, there are not

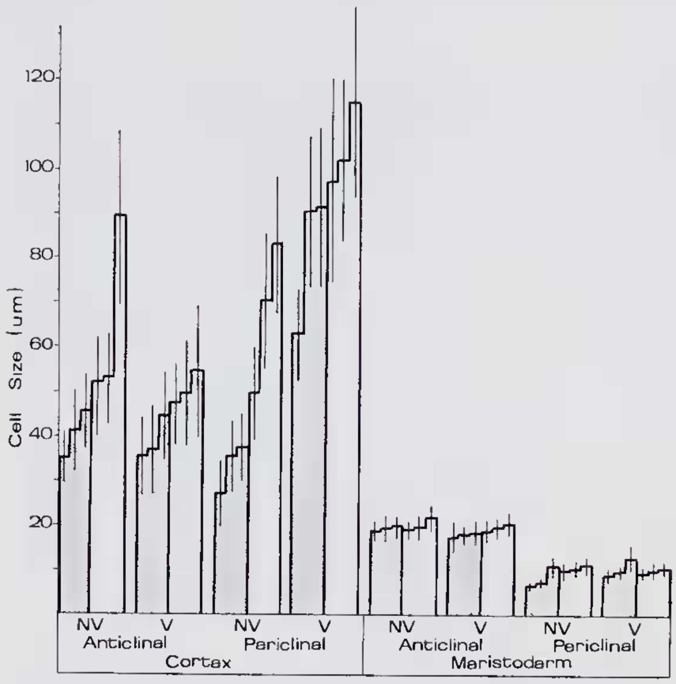

Figure 3.—Cell dimensions in vesiculate and non-vesiculate frond areas of three estuarine (shaded) and three oceanic thalli of *Hormophysa triquetra*. Anticlinal and periclinal indicate directions of cell measurement. V, vesiculate; NV, non-vesiculate. Standard deviation bars are shown.

only fewer meristoderm cell divisions as evidenced by the narrower frond and vesicle areas, but also smaller cortical cells. Although vesicle volumes were not compared because this study was based upon transverse sections of material, observations of longitudinal sections suggest that the above conclusions are applicable to this dimension as well. That is, the estuarine form differs from the oceanic form in its reduced cell enlargement and cell division capacities.

As for the taxonomic significance of the form variation in *Hormophysa triquetra,* there are several considerations. Firstly, the basic spiral growth pattern from a triangular apical cell, the pattern of initiation of laterals, and the pattern of vesicle formation are the same in all forms. Secondly there are transition forms between the morphological extremes. Therefore there seems little merit in formalizing varieties or ecads of *H. triquetra* at this time, particularly without the support of eco-physiological date. Studies of variation in *Ascophyllum* by Brinkhuis and Jones (1976) and Brinkhuis, Temple and Jones (1976) suggest the directions for further study of *H. triquetra.*

References

Berquist, P. L. (1959).—A statistical approach to the ecology of *Hormosira banksii. Bot. Mar.* 1: 22-53.

Brinkhuis, B. H. (1976).—The ecology of temperate salt-marsh fucoids. I. Occurrence and distribution of *Ascophyllum nodosum* ecads. *Mar. Biol.* 34: 325-338.

Brinkhuis, B. H., and R. F. Jones (1976).—The ecology of temperate salt-marsh fucoids. II. In situ growth of transplanted *Ascophyllum nodosum* ecads. *Mar. Biol.* 34: 339-348.

Brinkhuis, B. H., N. R. Temple and R. F. Jones (1976).—Photosynthesis and respiration of exposed salt-marsh fucoids. *Mar. Biol.* 34: 349-359.

Chapman, V. J. (1976).—Coastal Vegetation, Second Edition. Pergamon Press, Oxford. 292 p.

Gibb, D. C. (1967).—The free-living forms of *Ascophyllum nodosum* (L.) Le Jol. *J. Ecol.* 45: 49-83.

Johnson, A. (1967).—Studies in the conceptacle development and taxonomic position of *Cystoseira prolifera* J. Ag. *Bot. Mar.* 10: 134-140.

Mairh, O. P., and V. Krishnamurthy (1970).—Some observations on the morphology and development of *Hormophysa triquetra* (C. Ag.) Kuetzing. *Bot. Mar.* 13: 38-41.

Moss, B. (1971).—Meristems and morphogenesis in *Ascophyllum nodosum* ecad *mackaii* (Cotton). *Br. Phycol. J.* 6: 187-193.

Papenfuss, G. F. (1967).—The history, morphology and taxonomy of *Hormophysa* (Fucales: Cystoseiraceae). *Phytomorphology* 17: 42-47.

South, G. R., and R. D. Hill (1970).—Studies on marine algae of Newfoundland. I. Occurrence and distribution of free-living *Ascophyllum nodosum* in Newfoundland. *Can. J. Bot.* 48: 1697-1701.

Womersley, H. B. S. (1967).—A critical survey of the marine algae of Southern Australia. II. Phaeophyta. *Aust. J. Bot.* 15: 189-270.